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Original Articles.

MOTOR PATHS IN THE BRAIN AND CORD OF THE MONKEY.[1]

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These experiments[2] consisted in the removal of a single minute portion of cortex from one hemisphere (invariably the left). The animals were allowed to live after the operation for periods varying from 10 to 40 days, when they were killed, the brain and cord carefully removed, hardened in Müller's fluid and stained by the Marchi method. In each operation the greatest care was taken to secure perfect asepsis, and in no single case was there the slightest trace of septic infection. In all the experiments here reported the portion of cortex excised was taken from the so-called motor area; some from the face, some from the arm, and others from the leg area. The movement controlled by the portion removed was, in each case, determined by faradic excitation, the weakest possible current being used to obtain an uncomplicated movement. As is well known in electrical stimulation of the motor cortex, the stronger the current, or the longer continued, the more complex is the movement. In most cases the removal of so small a portion of cortex, generally from 2 to 4 mm. square, was followed by no apparent disturbance of function. In a few cases, mostly following removal of the area governing movements of the thumb, the operation was followed by slight temporary disturbance of function, rarely persisting more than a few days.

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[1] Read before the Philadelphia Neurological Society, November 28, 1898. For discussion on this paper, see p. 178.

[2] The experiments here described were done in the Pathological Laboratory of University College, London, and in the Anatomical Laboratory of Johns Hopkins University, Baltimore.

The amount of degeneration following the removal of so small a portion of the cortex was in some cases surprising, and although the effort was made to have the area removed always about the same size, the amount of degeneration, or rather the number of degenerated fibers, varied largely in the different animals. Another noticeable result was the difference in the size of the fibers depending upon the portion of cortex excised. The largest fibers were found following lesions in the highest portion of the brain near the top of the fissure of Rolando, that is, that portion of the cortex governing movements of the great toe. Fibers coming from those areas, however, were not all large, but were mixed with finer fibers in varying proportions. The average size of the fibers appeared to diminish in proportion to the distance of the lesion downward on the convexity of the brain. From lesions on the upper border of the fissure of Sylvius, near the lower extremity of the fissure of Rolando, the area controlling movements of the lips and mouth, the fibers were much finer; while from areas just anterior to this, excitation of which produces the rhythmical movement of mastication, and from the region still more anteriorly where the center for laryngeal movements is situated, the degenerating fibers were very fine, so fine in fact that it was almost impossible to trace their course by the Marchi method. This gradual decrease in the size of the axis-cylinders from above downward would seem to correspond to a similar decrease in the size of the pyramidal cells, as well as to bear some relation to the length of the axones.

The degeneration of what may be called association fibers following all these lesions was very considerable. They were all *subcortical,* as it was impossible to trace any degeneration within the substance of the cortex. This was probably because intracortical fibers in the monkey have little or no myelin. These subcortical fibers were both coarse and fine, and in some instances could be followed long distances from the lesion. Either coming from or passing to the cortex, they do not run close beneath it, but some little distance in the depth of the white substance. Possibly many of the finer of these fibers represent collaterals of the pyramidal fibers, but many are of a caliber equal to the largest pyramidal fibers proceeding directly from the lesion, and may rather be looked upon as axones arising in the portion of cortex removed. Others may have been subcortical fibers passing near the lesion which came in the way of the knife. In many cases, especially when the lesion was near the fissure of Rolando, these subcortical association fibers were particularly numerous passing under that fissure, connecting the cortex of the ascending frontal with that of the ascending parietal convolution. In no other instance do these experiments show such intimate anatomical relations between neighboring gyri. This is quite possibly due to the fact that most of the lesions were not far from the fissure of Rolando. The distribution of these fibers would seem to bear some possible relation to what Beevor and Horsley[3] termed the "absolute area of representation." Thus, in electrical stimulation of the cortex there is a "focus" for a certain definite movement, flexion of the hallux for example, a limited area, stimulation of which with a very weak current produces that simple uncomplicated movement. This focus is the center of a considerable cortical area, stimulation of which produces the same movement, but complicated with other and more complex movements. This larger area they term the "absolute area of representation." The distribution of subcortical association fibers was not, however, limited to such areas, but some fibers could be traced beyond the motor cortex into the silent areas. This was more particularly the case when the lesion was near the border of the motor area. Lesions of the ascending frontal convolution were very likely to give rise to some degeneration in the frontal gyri. Occasionally evidences of slight degeneration were found in the tempero-sphenoidal lobe and in the convolutions of the internal surface, but never in the occipital lobe.

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[3] Beevor and Horsley, Phil. Trans. Roy. Soc., of London, B. 1888.

In all cases scattered degenerated fibers crossed in the middle third of the corpus callosum to be distributed to the convolutions of the opposite hemisphere. This distribution, though generally less extensive than on the side of the lesion and much less in amount, was apparently quite symmetrical. In lesions of those areas controlling movements in which one would expect bilateral representation, such as the rhythmical movement of mastication, the distribution of blackened fibers to the convolutions of the two hemispheres seemed to be more nearly equal. The proportion of the blackened fibers crossing in the corpus callosum to the amount of degeneration proceeding from the lesion was not always constant. The callosal fibers were in most cases both coarse and fine. Often the coarser callosal fibers were quite as coarse as any found on the side of the lesion, from which it would appear probable that the callosal fibers are not made up exclusively of collaterals.

Proceeding inward or downward from the lesion, there was in each case a tract of blackened fibers consisting of either both coarse and fine fibers in varying proportions or, as before stated, in some cases of only very fine fibers. In passing through the centrum ovale on the way to the internal capsule these fibers became more or less scattered and were not again found as a distinct and separate bundle, but were always more or less mixed in with the healthy fibers. In the upper levels of the internal capsule their position seemed to depend very much on the site of the lesion. In the upper levels of the internal capsule above the level where the fibers begin to come in from the frontal lobe to form the anterior limb, levels in which the capsule has no distinct genu and all the fibers are transversely cut in a horizontal plane, fibers coming from lesions in the upper portions of the convexity, as leg and upper arm areas, were found in the posterior half, while fibers from lesions lower down on the convexity, as hand or facial areas, were in the anterior half. The former fibers passed downward and slightly forward, while the latter passed downward and rapidly backward until in the lower levels of the internal capsule all the degenerated pyramidal fibers coming from lesions in this series of experiments, facial as well as lower limb fibers, were found well within the limits of the middle third of the posterior limb. Within this area there was but slight tendency to a grouping of the fibers coming from any one portion of the cortex and that was so inconstant that it gave no hint of a law governing their arrangement. Beevor and Horsley[4] figure a certain methodical arrangement of the fibers in the monkey in the internal capsule based upon the results of electrical stimulation of the cut ends of the pyramidal fibers after the removal of successive segments of the brain from above downward. They group the fasciculi in the internal capsule from before backward, much in the same order and sequence as the excitable areas of the cortex are arranged from the fissure of Sylvius upward. This agrees closely with the results of electrical stimulation of the capsule obtained by Frank and Pitres[5] in the dog, except that the latter investigators obtained facial movements from stimulation of the most posterior as well as the most anterior of the excitable fibers of the capsule. Beevor and Horsley found constant overlapping of the excitable areas in the capsule, overlapping correspondingly as extensive as that observed in cortical areas. This is explained by the demonstration in these experiments of scattered degenerated fibers over the whole excitable area of the internal capsule following restricted lesions of widely separated areas of the motor cortex. If this arrangement holds good in the human brain, damage to fibers in the anterior portion of the capsule or about the genu, if in the upper levels would give rise to facial paresis; while small lesions a few mm. lower would be quite as likely to affect the upper or lower limb.

A large proportion of the finer fibers coming from these lesions passed from the posterior limb of the internal capsule into the thalamus, into which many of them could be followed for some distance. That these fibers are not collaterals given off by the pyramidal fibers as they passed through the capsule is shown by the fact that the fine degeneration in the capsule disappeared in proportion to the amount of degeneration passing into the thalamus. While these fine fibers were very much mixed up with the coarser fibers in the capsule, they were much more numerous posteriorly, often encroaching considerably upon the posterior third of the posterior limb.

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[4] Beevor and Horsley, Phil. Trans., B. 1890, p. 49.

[5] Frank and Pitres, Leçons sur les functions motrices du cerveau, etc., par Frank, Paris, 1887.

From here on we will follow the degeneration from these lesions to their destination in groups arranged according to the location of the lesion upon the cortex, taking first those degenerations resulting from a lesion in the hallux center. The degeneration had, as stated, suffered a considerable diminution by the passage of fibers, mostly fine, into the optic thalamus. In the crus the remaining degenerated fibers were situated in the middle third, not in a compact mass, but pretty evenly scattered over the whole area. Here they suffered a still further loss, many fibers passing from the dorsal border of the crus into the substantia nigra, where they could be traced but a short distance before they disappeared. The proportion of fibers passing to the substantia nigra varied in different cases. The movement of these fibers toward the border of the crus adjacent to the substantia nigra suggested an inversion of the apex of the triangle which is generally figured as representing the position of the pyramidal fibers in the middle third of the crus in man. In other cases the area containing degenerated fibers was more like an irregular parallelogram, equally extensive on the border of the crus contiguous to the optic tract as on that bordering the substantia nigra. The remaining fibers passed on through the pons and medulla, scattered over the entire cross section of the left pyramidal tract. There was nothing to suggest any diminution in the number of degenerated fibers in the passage through the pons and medulla. At the decussation of the pyramids the tract clearly divided, the majority of the degenerated fibers crossing to the lateral column of the opposite side, while the remainder, the proportion varying in different cases, passed to the lateral column of the same side. Some blackened fibers clearly remained in the left anterior column. They retained this position, bordering the anterior longitudinal fissure, throughout the cervical and dorsal cord, their disappearance in the lumbar region apparently corresponding to that of the degenerated fibers from the lateral columns. None of these fibers were observed to decussate.

Although it has been asserted that there is no direct pyramidal tract in animals, these results show clearly that it does exist in some monkeys, and it is quite possible that it varies as much in individual animals as Flechsig has shown that it does in man. At the time that some of these results were first published in the Proceedings of the Royal Society of London,[6] Muratoff[7] had already published similar observations upon the dog. The division of the pyramidal tract at the decussation has since been demonstrated in the cat, dog and monkey by numerous investigators, and that the same condition obtains in man has now been proved by the observations of Dejerine, Hoche and Risien Russell. The varying proportion of pyramidal fibers passing to the lateral column of the same side (homolateral as they are termed by Russell) may depend upon varying proportions of the direct pyramidal tract. Further investigation may show that the number of homolateral fibers bears some direct relation to the size of the direct tract. Such relations, however, would suggest a participation of the direct and homolateral tracts in bilateral representation, and this is not borne out by the observations of Hoche[8] and Risien Russell[9] in the ultimate decussation of the fibers of the direct tract. The number and relative proportion of degenerated fibers in the crossed tract of each side remained unchanged throughout the cervical and dorsal cord. In the lumbar enlargement they gradually diminished from above downward. Occasional fibers could be traced for some distance toward the anterior horn cells, though the oblique course taken by these fibers as they left the pyramidal tract made them difficult to follow. In no instance could they be traced to the large cells of the anterior horn. Throughout the lumbar enlargement fine fibers were found leaving the crossed tract, and they could be followed across the middle line into the gray matter of the opposite side. Most of these fibers appeared to cross in the posterior commissure. In this connection it may be remarked that Ramon y Cajal[10] states that fibers in the lateral column give off collaterals which cross to the other side of the cord in the posterior commissure.

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[6] Proc. Roy. Soc., 1894. Vol. 55, p. 208.

[7] Muratoff, Archiv. für Anat. und Entwickelungsgeschichte, 1893, p. 97.

[8] Hoche, Archiv. für Psych. Vol. XXVIII, p. 980.

[9] Russell, Brain, Summer Number, 1898.

[10] Cajal, L'anatomie fine de la moelle épinière, Berlin, 1895, p. 13.

The degeneration following lesions of the thumb center was always proportionately less than that proceeding from hallux centers and consisted, as a rule, of finer fibers. While a certain proportion of these were tolerably coarse, the proportion of fine fibers was also much greater. In these cases the degeneration in the crus was not so fairly in the middle third. As a rule it was displaced toward the outer third, often encroaching on its limits. The passage of degenerated fibers to the substantia nigra was much more extensive, in some cases complete, so that below the crus no degenerated fibers could be found. In those cases in which degeneration could be traced on through the pons and medulla, the number of these fibers grew constantly less. Here and there single blackened fibers could be found leaving the pyramidal tract, but they soon disappeared and their destination could not be demonstrated. In consideration of the proximity of the facial area to these lesions, and the very considerable overlapping of all motor cortical areas, as demonstrated in electrical stimulation of the cortex, it is altogether probable that these lesions destroyed some cells connected with the facial nuclei. This assumption is strengthened by the fact that in some lesions of the facial area as far downward as the upper border of the fissure of Sylvius, a few degenerated fibers were traced into the cervical cord. Only in one instance was there a division of the degenerated fibers at the decussation of the pyramids following lesion of the thumb center. In that case very few fibers passed to the lateral column of the same side, but there were also in the same case a few degenerated fibers in the direct tract along the border of the anterior longitudinal fissure. The remaining blackened fibers in each crossed tract were very evenly scattered over the area allotted to each. These degenerated fibers and the few remaining in the direct tract in one animal maintained their numbers and relations until they reached the level of the seventh or eighth cervical root where they began to disappear. From this level downward to the level of the third dorsal root the degenerated fibers disappeared steadily and gradually, and at the level of the third dorsal root there were none left. As was noted in lesions of the hallux center, there was a movement of fine blackened fibers from the crossed pyramidal tract transversely across the cord, simultaneous with and corresponding to the disappearance of the degeneration from that tract. Most of these fibers could be traced nearly to the median line, and some could be distinctly seen to cross in the posterior commissure. Such fibers were only seen in those levels of the cord where degenerated fibers appeared to end, from which it would appear that if pyramidal fibers do give off such collaterals, it is only just before their termination. In these experiments the blackened fibers could be followed some distance in the direction of, but never as far as, the anterior horn cells. This could not be expected, the Marchi being essentially a fat stain and only affecting the fragments of broken-down myelin. The finer the nerve fibril and the more attenuated the medullary sheath, the smaller and more widely separated are the fat droplets. Thus, the chain of blackened fat globules would probably disappear some distance short of the terminal arborification of the nerve fiber.

Following lesions of the facial area the degenerated fibers were found in the crus as in the internal capsule scattered over the same area as those from other lesions, that is, in the middle third of the crus. There was no apparent grouping of these fibers toward the mesial portion of this area. In one case of lesion in the Rolandic operculum close upon the upper border of the fissure of Sylvius, and slightly behind the lower extremity of the fissure of Rolando, there was a steady migration of blackened fibers, a few at a time, from the middle third of the crus to the extreme outer border of the lateral pontine bundle, from whence they passed into the capsule of the corpora quadrigemina. This was observed in one instance only. In one instance a few fibers from a lesion of the very uppermost portion of the facial area were observed to pass from the pyramidal tract into the subthalamic region, and in one other case a few blackened fibers were traced to the substantia nigra.

In many cases degeneration from lesions of the facial area could not be traced as far as the pons, although in each case the characteristic facial movement was obtained by electrical stimulation before the removal of the small portion of cortex. In other cases the amount of degeneration in the pyramidal tract in the pons and medulla was very considerable. The distribution of degenerated fibers to the large-celled nuclei of the pons and medulla was most noteworthy. These fibers began to leave the pyramid in the upper levels of the pons above the level of the motor nucleus of the fifth, where a few single fibers were seen now and then leaving the most dorsal of the pontine bundles of the left side and plunging into the mesial fillet about midway between its mesial and lateral extremities. These fibers disappeared before reaching the dorsal border of the fillet. From this level downward through the pons a few blackened fibers pursued the same course, but the aggregate number leaving the area of degeneration in the pons was small. In the level of the exit of the auditory nerve many blackened fibers began to leave the left pyramid, always as single fibers, mostly from the mesial portion of its dorsal border. They entered the tegmentum and turned downward for a short distance, when they again turned and ran transversely and obliquely through the tegmentum to the neighborhood of the facial nucleus of each side. In no case could a blackened fiber be shown to run into the nucleus or to come in contact with a motor cell. This, of course, would be impossible unless the fiber retained its medullary sheath to its termination. It was only the very uppermost of these fibers that turned downward again after leaving the pyramid. In all the lower levels they passed from the left pyramid directly toward the facial nucleus of either the right or left side. The majority of these fibers leaving the pyramid near the raphe crossed it and ran to the neighborhood of the facial nucleus of the right side. A smaller number of blackened fibers were soon found leaving the pyramid near its external or lateral border. Most of these fibers could be traced almost to the facial nucleus of the same side, but a small number crossed through the tegmentum to a point in the raphe considerably dorsal to that crossed by the fibers leaving the pyramid more mesially, where they crossed and ran toward the facial nucleus of the opposite side. Of all the blackened fibers leaving the pyramid in these levels the majority apparently went to the nucleus of the opposite side. As those levels were reached in which the inferior olive is well developed no blackened fibers were found leaving the pyramid except from the mesial portion near the raphe. In one instance blackened fibers from the left pyramid crossed the raphe and ran transversely through the right pyramid and disappeared. The majority of these fibers left the pyramid in the levels of the facial nuclei, but occasional fibers passed from the mesial border of the pyramid as low as the decussation of the fillet. These fibers apparently went to the nucleus ambiguus of each side, somewhat in the same proportion as to the facial nuclei, the majority to the opposite side. As before mentioned, a small number of blackened fibers were found at lower levels, even as far down as the seventh or eighth cervical root. This probably explains the arm, hand and finger movements often obtained by stimulation of the facial area. The movements controlled by the cortex are entirely associated movements, and such movements must obviously be provided for either by independent fibers communicating directly with the spinal centers of the various movements, or by association fibers connecting cortical areas. It is altogether probable that the latter method is amply provided for in man, where the development of association tracts is the most remarkable feature of brain anatomy, but these experiments seem to prove that in the monkey pyramidal cells exist in widely separated portions of the motor cortex that may directly control, to a greater or less extent, the same groups of muscles.

LEGENDS.

FIG. I. Horizontal section through the lower level of the internal capsule, showing location and extent of degeneration in the posterior limb following excision of a portion of the cortex from the hallux center of the left hemisphere.

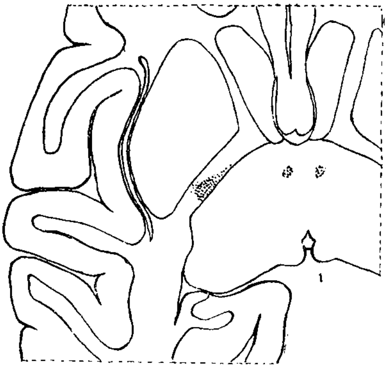
FIG. II. Horizontal section through the lower level of the internal capsule, showing location and extent of degeneration in the posterior limb following excision of a portion of the cortex from the thumb center of left hemisphere.

FIG. III. Horizontal section through the lower level of the internal capsule, showing location and extent of degeneration in the posterior limb following excision of a portion of the cortex of the left hemisphere from the upper portion of the facial area just anterior to the Rolandic fissure.

FIG. IV. Horizontal section through the crus, showing location and extent of degeneration following excision of hallux center.

FIG. V. Horizontal section through the crus, showing location and extent of degeneration following excision of the thumb center.

FIG. VI. Horizontal section through the crus, showing location and extent of degeneration following excision of the facial center. Same lesion as in Fig. III.



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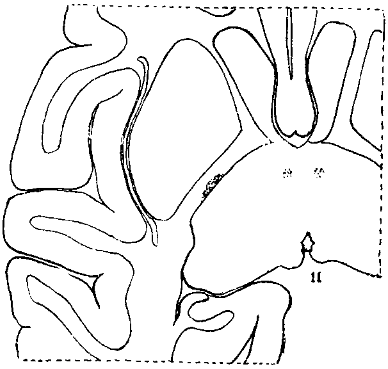

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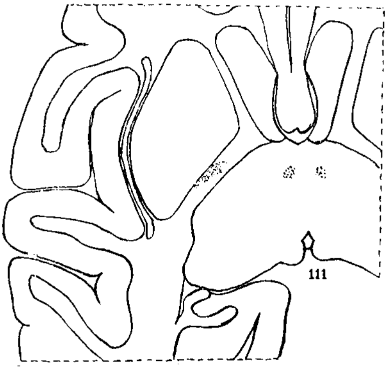

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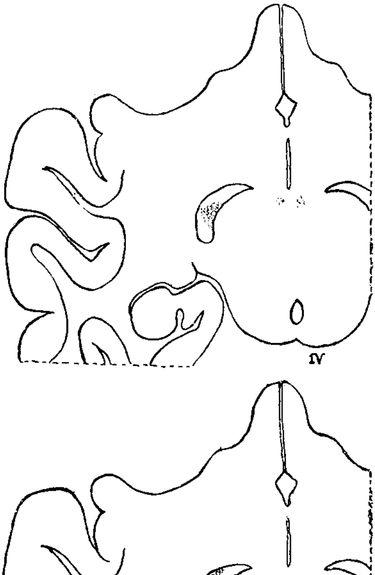

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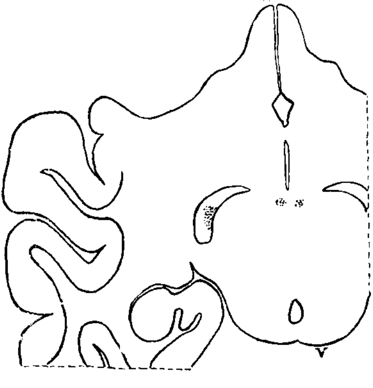

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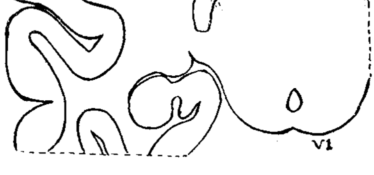

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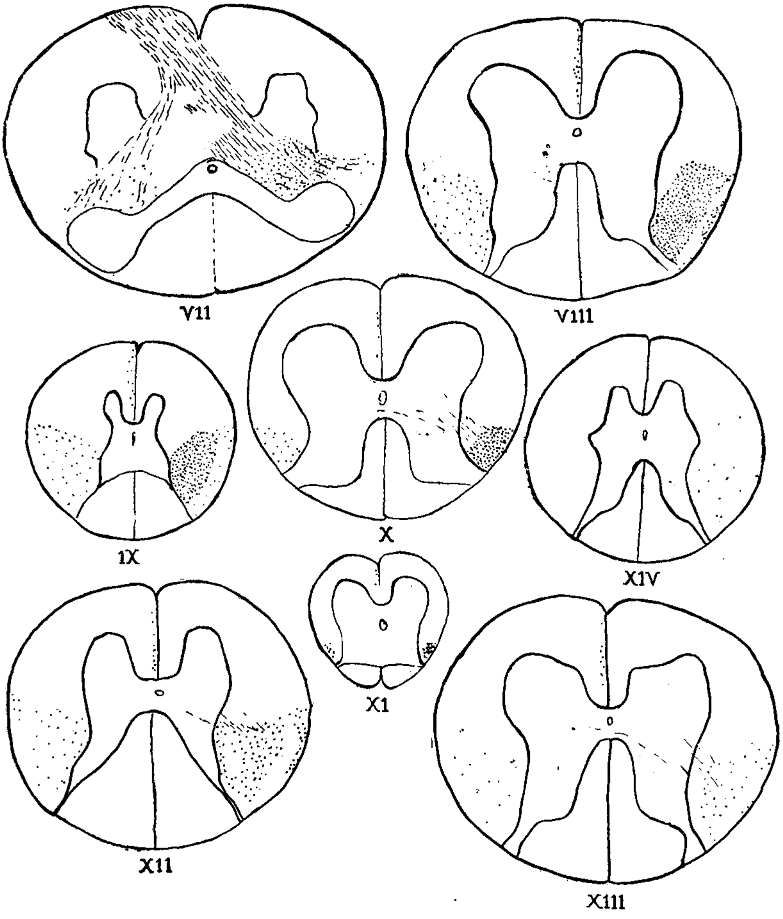

FIGS. VII, VIII, IX, X, XI. Transverse sections of the spinal cord, showing extent and distribution of degeneration at the level of the respective spinal roots following excision of the hallux center. (VII, motor decussation; VIII, 5 c.; IX, 6 t.; X, 2 l.; XI, 3 s.).

FIGS. XII, XIII, XIV. Transverse sections of the spinal cord, showing extent and distribution of degeneration at the level of the respective spinal roots following excision of the thumb center. (XII, 2 c.; XIII, 6 c.; XIV, 2 t.)